TENDRILS OF SMILAX[1]

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(WITH PLATE XXII)

The nature of the tendrils of *Smilax* has excited perhaps more controversy than almost any other problem arising out of the normal vegetative morphology of flowering plants. It is unnecessary to deal here in detail with the voluminous literature which has grown up about the subject, since this task has been excellently performed by DOMIN (4), who himself holds the opinion that the tendrils are trichome structures, an opinion which does not seem to the writer to be well founded. It will suffice to group together the various alternative views which he has enumerated, and to attempt to test them, from the standpoint of the phyllode theory (1), by a study of a typical species, *Smilax herbacea* L. (fig. 1). The views which different authors have promulgated may be considered as follows, under five heads:

1. That the *Smilax* tendrils are metamorphosed stipules, or outgrowths of the apical region of the leaf-sheath.

Both these possibilities seem to be excluded by the fact that the tendrils arise from the petiole, immediately above the sheath, it is true, but entirely disconnected from it both externally and as regards their vascular system.

2. That the *Smilax* tendrils represent a bipartite ligule, each tendril being a demi-ligule.

This alternative is ruled out because, as GLÜCK (5) and DOMIN (4) have shown, there is occasionally a definite ligule in addition to the tendrils. It is also discounted for the same reasons that make the first view untenable.

3. That the *Smilax* tendrils are either metamorphosed leaflets, segments, or lobes of a compound leaf, or lateral free nerves which become detached before the others.

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If any of these related alternatives held good, we should expect to find the vascular structure of the tendril showing some affinity with the vascular structure of the midrib or lateral veins of the "lamina" of the *Smilax* leaf. The midrib and lateral veins of the blade, however, are each characterized by an arc of bundles (fig. 4), while the tendrils have an irregular closed ring (fig. 3 *B*).

4. That the *Smilax* tendrils are metamorphosed trichomes or emergences.

The high development of the vascular system of the tendrils seems to make it impossible to accept this theory. The emergences on the stem of *Smilax* itself, which on this view must be homologous with the tendrils, are non-vascular, as are the paired glands at the base of the leaf of *Tamus communis* L., whose position at first glance suggests a comparison with the tendrils of *Smilax*.

5. That the tendrils of *Smilax* represent "un double prolongement latéral des éléments cellulo-vasculaires du pétiole."

This view, which was suggested by CLOS (2) more than half a century ago, and has been more recently supported by GLÜCK (5), seems to contain the germ of the true explanation, although, in the form in which CLOS enunciates it, it is essentially descriptive rather than morphological. The writer wishes to propose a related but more comprehensive view, which interprets each of the tendrils of *Smilax* as equivalent in morphological value to the petiole, and as having originated through a dédoublement or chorisis of that organ.

An analogy may perhaps be suggested with the stamen phalanges of *Hypericum Elodes* Huds., which sometimes consist of three members, and which very probably have arisen by secondary chorisis of an ancestral single stamen. A closer analogy is indicated by QUEVA'S (7) comparison between the anatomy and insertion of the tendrils of *Smilax* and the stalks of the leaflets of certain Dioscoreaceae with compound leaves. It seems by no means impossible that, in this family, the compound character of the leaf may also be due to chorisis of the petiole giving rise to three equivalent organs.[1]

[1] The writer hopes to deal in a later paper with the general subject of "compound" leaves among monocotyledons, and to discuss the part which chorisis may have played in their origin.

It is unnecessary to follow the relations of the vascular system of the petiole and tendril of *Smilax* in detail, since this has already been done by QUEVA. The general equivalence of the vascular structure in these organs is shown in fig. 3 *B*. It may perhaps be objected that the occurrence of a ring of bundles in the *Smilax* tendril, instead of being an indication of homology with the petiole, may merely represent that skeletal arrangement which best enables the tendril to perform its special function. The weight of this criticism, however, is lessened when we realize that in the leaf tendrils of another member of the Liliaceae (*Gloriosa superba* L., fig. 6), which approach radial symmetry in their external form quite as closely as do the tendrils of *Smilax*, the plan of the vascular system remains purely dorsiventral, although the amount of xylem increases considerably in passing from the lamina to the tendril (figs. 7, 8). The leaf tendrils of *Fritillaria verticillata* Ledebour, and of *Polygonatum cirrhifolium* Royle, resemble that of *Gloriosa* in structure.

According to the phyllode theory advocated by the writer (1), the blade of *Smilax* is not equivalent to the lamina of a dicotyledon, but is merely a "pseudo-lamina" representing an expansion of the upper region of the petiole. The thickened tip (fig. 5 *ap*) which characterizes the blade of some members of the genus, for example *S. mauritanica* Poir., is possibly the last relic of the unexpanded petiolar apex. Each tendril on this interpretation is equivalent to the *petiole+pseudo-lamina*. On the other hand, in *Gloriosa* the leaf seems to be reduced to the sheath or leaf-base alone, the tendril representing the specialized tip of this leaf-base.

Petiolar tendrils, with the blade entirely, or almost entirely, aborted, are not unknown among dicotyledons, as, for example, the first leaves of a species of *Tropaeolum* described by DARWIN (3). In connection with *Smilax*, it is perhaps significant that a tendency to torsion of the petiole or leaf-base is by no means rare among monocotyledons. Cases are known, for instance, in the Commelinaceae, Amaryllidaceae, Zingiberaceae, and Gramineae, as well as in the Liliaceae, to which *Smilax* belongs (6). In most of these instances the torsion, even in the extremest examples, merely leads to resupination of the leaf; but in *Gloriosa* this power of twisting of a region which, although now apical, seems in reality to be part of the leaf-base, has been utilized in tendril formation. It is interesting that *Polygonatum* includes both species with twisted leaves and also species whose leaves have tendril apices resembling those of *Gloriosa*. Similarly in *Smilax* the torsion capacity of the petiole seems to have fulfilled itself on specialized lines in the production of a climbing organ.

It may be noted in passing that the blade of *Smilax* often conforms to a shape which is one of the most characteristic among those adopted by the pseudo-lamina of monocotyledons, its outline being entire and more or less ovate, with a base which is cordate or somewhat sagittate (fig. 1). Forms of this type, as has been pointed out in a previous paper (1), are not only known in the Liliaceae, but recur in the Alismaceae, Pontederiaceae, Dioscoreaceae, Araceae, and Orchidaceae. This list may now be increased by the addition of *Cyanastrum cordifolium* Oliver, of the Haemodoraceae, and certain species of *Commelina* among the Commelinaceae.

To the writer, the whole organization of the leaf of *Smilax* is best explained according to the phyllode theory, and the interpretation suggested has been reached from this standpoint. At the same time, however, the view here propounded, of the origin of the tendrils of this genus through chorisis of the petiole, in no way depends upon this general theory. There is nothing to prevent its independent acceptance by those who do not share the conviction that the leaves of monocotyledons are invariably of the nature of petiolar or leaf-base phyllodes.

Summary

In this paper the conflicting views hitherto held regarding the nature of the tendrils of *Smilax* are briefly considered, and it is concluded, on grounds of anatomy and external morphology, that these tendrils are equivalent to the petiole in morphological value, and have arisen through chorisis or dédoublement of that organ.

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EXPLANATION OF PLATE XXII

In all sections xylem is indicated in black, and phloem and undifferentiated bundles in white.

FIG. 1.—*Smilax herbacea* L.: single leaf showing sheath (*s*), tendrils (*t*), and petiole (*p*); $\times\frac{2}{3}$.

FIG. 2.—*Smilax herbacea* L.: *A*, transverse section of very young lamina and accompanying tendrils; vascular tissue too young to be well differentiated; petiole as yet undeveloped; *B*, actual attachment of tendrils; these sections illustrate large size of tendrils relative to lamina in embryonic stage; $\times 31$ circa.

FIG. 3.—*Smilax herbacea* L.: transverse sections of mature leaf; *A*, through leaf sheath; *B*, through petiole and tendrils, showing relative orientation of organs; $\times 19$ circa.

FIG. 4.—*Smilax herbacea* L.: transverse section close to base of lamina passing through midrib (*mr*) and main lateral (*ml*); $\times 19$ circa.

FIG. 5.—*Smilax mauritanica* Poir.: *A*, pseudo-lamina with thickened apex (*ap*); $\times\frac{2}{3}$; *B*, transverse section through apex; $\times 19$ circa.

FIG. 6.—*Gloriosa superba* L.: leaf with apical tendril; $\times\frac{2}{3}$.

FIG. 7.—*Gloriosa superba* L.: transverse section through tendril; lateral veins fused so that only midrib and 2 laterals show; $\times 31$ circa.

FIG. 8.—*Gloriosa superba* L.: transverse sections of another leaf showing transition from apex of limb (*A*) to base of tendril (*C*); $\times 31$ circa.